INTERSPECIFIC COMPETITION FOR NEST CAVITIES BY INTRODUCED LOVEBIRDS *AGAPORNIS* SP. AT LAKE NAIVASHA, KENYA

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Hybrid Fischer's x Yellow-collared Lovebirds *Agapornis fischeri* x *personata* were introduced to Lake Naivasha, Kenya in the late 1950s by private aviary owners. The birds' ability to breed in captivity forced the owners to release them into the wild and, in 1986, their numbers were estimated at just under 6000 (Thompson, in prep.). Hybrid lovebirds have been released elsewhere in Kenya (Cunningham-van Someren 1975) and are now found in Nairobi, Kiserian, the Ngong Hills, Meru, Embu, Nakuru, Molo, Kisumu and parts of the Kenya coast (G.R. Cunningham-van Someren, pers. comm.). Due to this wide distribution, Lake Naivasha was chosen as a convenient site at which to study competitive interspecific interactions between lovebirds and other cavity-nesting species.

Competition for nesting cavities among hole-nesting birds has been recorded both in natural avian communities and between introduced and native species. The introduction into North America of the European Starling *Sturnus vulgaris* and the House Sparrow *Passer domesticus* has forced Eastern Bluebirds *Sialia sialis* to nest almost exclusively in nest-boxes provided by man (Gowaty 1985). Woodpeckers, such as the Northern Flicker *Colaptes auratus* and the Red-headed Woodpecker *Melanerpes erythrocephalus* have also probably been adversely affected (Short 1979). Von Haartman (1957) was among the first to suggest that hole-nesting birds (his study only covered passerines in temperate regions) are limited by the availability of nest sites, and he placed more importance on these than on food availability as an ecological limiting factor determining the maximum number of nesting pairs.

Evidence of competition for nest holes among birds comes from both behavioural and experimental data. Interspecifically directed aggression among hole-nesting birds has been commonly noted (von Haartman 1957, Orians & Willson 1964, Welty 1964, Armstrong 1965, Short 1979, 1982) as being caused by competition for a limited supply of suitable holes or cavities. The Eurasian Wryneck *Jynx torquilla*, for example, will even empty out the nesting material and eggs of another bird (von Haartman 1957). Evidence also includes the densities of hole-nesting birds increasing with the provision of nest boxes (Welty 1964, von Haartman 1957) and nesting pairs, when removed from their hole, immediately being replaced by, until then, non-breeding individuals. Brush (1983), however, found competition between hole-nesters to be unimportant since cavities were not fully utilized and did not limit breeding despite extensive habitat and nesting season overlap. He concluded, though, that interference competition may be more crucial in situations where nest sites are in short supply.

Lovebirds have previously been noted as occupying and probably breeding in other species' nests (Moreau 1948), including the Rufous-tailed Weaver *Histurgops ruficauda* and old swift's nests (Forshaw 1981), and a barbet's nesting hole (Mackworth-Praed & Grant 1952). Whether their competition involved usurpation of the former species was not mentioned. To determine the extent to which the introduced lovebirds have interfered with

the success of resident hole-nesting birds, an attempt was made to answer four questions: 1. What is the overlap between lovebirds and other hole-nesters in the preferred nest-/roost-hole type? 2. How aggressive are lovebirds towards other species? 3. Are lovebirds capable of usurping other hole-nesters from their holes? 4. Are some hole-nesting species absent from the Lake Naivasha forest where they have commonly been recorded in the past?

METHODS

Lake Naivasha lies in the Kenyan Rift Valley between latitudes 0°50S and 0°40S and longitudes 36°15E and 36°25E at an altitude of about 1890 m. Unlike most other nearby Rift Valley lakes, which are strongly alkaline, Lake Naivasha is fresh. The climate of the area is warm and semi-arid receiving a total average annual rainfall of some 630 mm. The study area included the strip of fever tree Acacia xanthophloea woodland which immediately surrounds the lake, an area of approximately 1790 ha. Outside the forested area, the rising land abruptly gives way to semi-arid Tarchonanthus camphoratus bushland.

During this study 16 species of cavity-nesters representing nine families were seen. These were the Grey Woodpecker *Mesopicos goertae*, Nubian Woodpecker *Campethera nubica*, Bearded Woodpecker *Thripias namaquus*, Cardinal Woodpecker *Dendropicos fuscescens*, Red-throated Wryneck *Jynx ruficollis*, Pearl-spotted Owlet *Glaucidium perlatum*, Woodland Kingfisher *Halcyon senegalensis*, Lilac-breasted Roller *Coracias caudata*, Hoopoe *Upupa epops*, Green Wood Hoopoe *Phoeniculus purpureus*, Grey Hornbill *Tockus nasutus*, Red-fronted Barbet *Lybius diadematus*, White-bellied Tit *Parus albiventris*, Blue-eared Glossy Starling *Lamprotornis chalybaeus*, Rüppell's Long-tailed Glossy Starling *L. purpuropterus* and the Superb Starling *Spreo superbus*.

Virtually the only tree available for nest cavity excavation is the fever tree. It is a flat-topped, fast-growing species up to 24 m high (Government Printer 1936) with a short life expectancy of about 40 years (J. Hayes, pers. comm.). A comparison of aerial photographs from 1969 and 1984 shows that the extent of fever tree distribution and overall maturity of the forest is increasing, probably due to a government ban on tree felling.

In order to identify occupied roosting or nest holes, daily watches were kept on likely cavities during the last hour of daylight. Information was recorded on the occupying species, height above ground level (estimated visually) and cavity type. A list of interspecific encounters between lovebirds and other species was compiled to determine any dominance hierarchy. The contestants in each encounter were judged 'winners' or 'losers', the 'winner' always being the aggressor while the 'looser' being the bird driven away or forced to retreat. Observations were recorded from all times of the day.

RESULTS AND DISCUSSION

Cavity types fell into three well defined categories: firstly, many hole-nesters used the end of a broken branch or a crevice along its length to nest in, excavating the central rotten wood to form a cavity; secondly, a tree-knot or small lateral outgrowth sometimes forms, allowing entry by birds into the main trunk; lastly, holes excavated and occupied by woodpeckers (almost always in dead wood) or taken over by other hole-nesting species.

A total of 94 cavities occupied by birds was positively identified, 57 of which were used by lovebirds. Of these 57, 58 per cent were of the broken branch type, 14 per cent of the tree-knot type and 28 per cent old woodpecker holes. Average heights above ground level for the three cavity types were 6.2, 7.3 and 6.2 m respectively. Many other holes that were watched were either unoccupied or used by tree mice *Apodemus* sp.

The remaining species for which cavities were located are listed below with the number of cavities observed, cavity type and average height above ground level.

Pearl-spotted Owlet—one cavity in an abandoned woodpecker hole; 5 m.
Woodland Kingfisher—two cavities, both in woodpecker holes; 7 m.
Lilac-breasted Roller—two cavities, both in woodpecker holes; 15.5 m.
Hoopoe—one cavity in a tree-knot; 8 m.
Green Wood Hoopoe—three cavities, one in a broken branch, one in a tree-knot and one in a woodpecker hole; 6.6 m.
Red-fronted Barbet—one cavity in an abandoned woodpecker hole; 4 m.
Grey Woodpecker—13 holes located, all conventional woodpecker holes; 5 m.
Nubian Woodpecker—one hole, conventional woodpecker type; 2 m.
Bearded Woodpecker—four holes, conventional woodpecker type; 10 m.
Cardinal Woodpecker—two holes, one conventional, the other in a cavity at the junction of a dead branch and the tree trunk; 5 m.
Blue-eared Glossy Starling—three cavities, one in each type; 4 m.
Superb Starling—two cavities, one in a broken branch and one in a tree-knot; 8.5 m.

There was no obvious preference by lovebirds for any particular cavity type or height above ground level used. They have been described as indiscriminate cavity-nesters (Moreau 1948) and therefore all cavity nesting species are exposed to competition for nest sites with lovebirds. The occurrence of many apparently unoccupied holes does not necessarily imply an overabundance of them. They may be occupied by a variety of organisms from small mammals to insects or be unsuitable for occupation due to the presence of invertebrates, including parasites, after previous use by birds (Short 1979).

Except in maize *Zea mays* fields—maize forms a significant proportion of their diet at Naivasha—lovebirds were seen to aggress on another bird species only once. This occurred between a Grey Woodpecker and a group of lovebirds using holes 20 cm apart on the same branch. Individual lovebirds were seen twice to approach the woodpeckers' hole and peer into it while the woodpecker retreated inside. Another Grey Woodpecker was perched on a branch near the hole but with the arrival of a lovebird there, flew to an adjacent tree trunk 2 m away. At one time nine lovebirds were perched on a branch a metre above the woodpecker hole. Although perhaps not a clear case of aggression, the woodpecker appeared to be intimidated by the lovebirds' presence and certainly did not retaliate by attacking.

At Naivasha, lovebirds are a comparatively timid species and were observed as clear 'losers' in encounters with Lilac-breasted Rollers three times, a Green Wood Hoopoe once, a Drongo *Dicrurus adsimilis* once, a Red-fronted Barbet once, a Grey Woodpecker once, a Blue-eared Glossy Starling once, a Superb Starling once and a Grey-backed Fiscal

Lanius excubitorius once. However, it is their flocking behaviour which, at least in part, compensates for their lack of aggressiveness. Dilger (1960) concluded that although nest cavity defence is apparently non-existent in *A. fischeri* and *A. personata*, it may be adequately compensated for by increased mobbing activity. Although Dilger performed his experiments under laboratory conditions, lovebirds at Naivasha did become more aggressive when supported by other individuals, as described above in the encounter with the Grey Woodpecker. Furthermore, according to a local resident, a pair of Lilac-breasted Rollers which had nested regularly on his land, was forced to leave due to the sheer numbers of lovebirds. While a very aggressive species, Lilac-breasted Rollers are shy at the nest and desert easily (Mackworth-Praed & Grant 1962). High lovebird densities may also cause desertion by increased aggressive activity of the defending species and the consequent attraction of predators (Short 1982).

The only situation where lovebirds were consistently overtly aggressive towards other species was in maize fields. Orians & Willson (1964) reported a similar behavioural reversal between Red-winged Blackbirds *Agelaius phoeniceus* and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* in North America between feeding grounds and breeding territories. They argued that selection should favour heightened aggression in habits where each respective species is better adapted since the more suitable the habitat, the greater the benefits of fighting for it. Certainly lovebirds are better equipped to open maize ears but the other maize pests, such as weavers Ploceidae and mousebirds Coliidae, may also have learned to allow lovebirds first access, enabling a more efficient exploitation of the food source. As such, this reversal in aggressiveness may also be due to a reduction in aggression of other species usually dominant over lovebirds. A learned component is implied, given the relatively short time for selection to act since the introduction of lovebirds to the area.

While they are probably not capable of hole usurpation by sheer physical means, lovebirds may exert a competitive threat for hole possession by more indirect methods. During the day they will investigate and modify the cavities of other hole-nesters. For example, lovebirds were observed bringing to a Green Wood Hoopoe's nest, acacia twigs (which lovebirds use in the construction of their own nests) which the wood hoopoes removed on their return to roost. Similar behaviour has been observed in the Tityras *Tityra semifasciata* and *T. inquisitor* by Skutch (1969 quoted by Short 1979). They are successful in usurping woodpeckers by filling their holes with leaves and debris so the woodpeckers eventually tire of removing it and abandon the nest. Lovebirds were also seen to enter and peck away at the entrance of an old woodpecker hole taken over by a Pearl-spotted Owlet. Alteration of the entrance hole by usurping species has also been noted before (Short 1979, Lanning & Shiflett 1983).

Lovebirds are persistent in their efforts at nest usurpation. Three lovebirds were seen investigating a Red-fronted Barbet's hole—one actually entering for some minutes. On the return of the barbet they were forced to leave by its aggressive behaviour but four months later, lovebirds were still investigating the hole. Such persistence may eventually cause a harassed bird to give up its hole. However, Lanning & Shiflett (1983) have concluded in their study on Thick-billed Parrots *Rhynchopsitta pachyrhyncha* that

investigation of cavities may occur for reasons other than their usurpation. This possibly explains the long time period over which the lovebirds has been investigating the barbet's hole without usurping it. Nevertheless, it is probably this tendency towards hole investigation which attracts aggression from other hole-nesters. Woodpeckers, for example, are able to 'recognize' potential nest competitors and will readily attack them even when there is no direct threat to the nesting hole (Short 1979).

Lovebirds may indirectly prevent woodpeckers from excavating new holes due to the lovebird's habit of burrowing down and nesting in the central core of dead branches. By taking up much of the branches length as an entrance tunnel and nest cavity, woodpeckers are prevented from excavating a hole, especially if mobbed by the inhabiting lovebirds. Old woodpecker holes are used by many other species of hole-nesters so that the lovebirds are also preventing the excavation of potential homes for a variety of species.

Lovebirds permanently occupy their various cavities throughout the year, unlike some other hole-nesters. This and the substantial modification of the nesting cavity prevents sequential use of the hole by several hole-nesters in the same season—an adaptation suggested to be important for the reduction of aggression and nest interference (Brush 1983). Woodpeckers are particularly vulnerable because of their use of several alternative holes, which are vulnerable to usurpation by lovebirds (L.L. Short, pers. comm.). Alternate holes are especially important for fledgling woodpeckers and the risk of predation is increased without them. Furthermore, the majority of woodpecker holes at Naivasha are excavated in dead wood thus increasing the risk of usurpation since the entrance hole can be enlarged more easily than if it were excavated in live wood (Short 1979).

All hole-nesting species previously recorded at Lake Naivasha were seen but some were less common than expected. These were the Cardinal Woodpecker seen four times and the Red-fronted Barbet seen three times. Both are similar in size to lovebirds and hence most likely to draw the greatest degree of competition (Short 1979). Furthermore, the Cardinal Woodpecker was the only woodpecker seen to sometimes roost in holes similar to those used by lovebirds. It is possible that the densities of all hole-nesters have declined but no data are available on their densities before the introduction of lovebirds.

Lovebirds have successfully established themselves at Naivasha and it is hard to believe that other hole-nesters have not suffered as a result. Slobodkin (1961) has argued that for an invading species to establish itself, its ecological niche must have been previously unoccupied or inefficiently exploited and that either situation is less likely in a complex community. Since lovebirds have indeed established themselves in a complex community where every niche is likely to have been utilized, an element of competition at the expense of other species is implied.

It is likely that the increasing Naivasha and Kenyan lovebird populations will have a serious effect on indigenous cavity-nesters. This, and their status as a pest of maize (Thompson, in prep.) and their great adaptability to new habitats conferred to them by being hybrids, make them a bird worthy of monitoring in the future.

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